

Taxonomy of the Reticulate *Vandenboschia radicans* Complex (Hymenophyllaceae) in Japan

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The taxonomy of the *Vandenboschia radicans* complex in the Japanese Archipelago was revised to reflect recent DNA and ploidy analyses. Four diploid species (*V. kalamocarpa* comb. nov., *V. nipponica* comb. nov., *V. birmanica* and *V. subclathrata*), four tetraploid (amphidiploid) species (*V. orientalis*, *V. hokurikuensis* sp. nov., *V. miuraensis* sp. nov. and *V. oshimensis* stat. nov.) and four hybrids are recognized. A key to the species excluding the hybrids is given.

Key words: hybrid, reticulate evolution, taxonomy, *Vandenboschia*

Vandenboschia Copel. is a genus of filmy ferns in tropical and temperate regions worldwide (Ebihara *et al.* 2006a). *Vandenboschia radicans* (Sw.) Copel., the type species of the genus, and its allies form a complex of morphologically ill-defined local species. Within the entire range of the complex, particular morphological variation is observed in the Japanese Archipelago. Our study employed nuclear/chloroplast DNA and ploidy analyses to elucidated the reticulate evolutionary history of the complex. The complex originated from at least three morphologically distinct diploid species (Ebihara *et al.* 2005). Although morphology-based identification is not always possible when intermediate taxa (hybrids and amphidiploids of hybrid origin) are included, providing names for the plants is necessary for communicating the findings.

Materials and methods

Taxonomic concepts

The taxonomic units are based on genomic formulas proposed by Ebihara *et al.* (2005, 2006b). In this paper, 65 samples of newly identi-

fied genomic formulas are provided (Appendix; methods for DNA and ploidy analyses follow Ebihara *et al.* 2005). In some cases, two or more different genomic formulas are combined under a single name based on the following:

- 1) Sterile lineages consisting of multiple genomes derived from two or more species (see the policy 2) are treated as hybrids, otherwise the lineages are treated as species.
- 2) Each of the α , β , γ and δ genomes is treated as the genome of a distinct species (see Ebihara *et al.* 2005). Plants with the α genome from Iriomote Island, Okinawa Pref., are treated as a distinct species based on morphology.
- 3) Autopolyploids that share the same genome (e.g., $\alpha\alpha$ and $\alpha\alpha\alpha$) are treated as the same species as their diploid progenitors.
- 4) Amphidiploids of hybrid origin, but with restored fertility by genome doubling are treated as species. To confirm fertility, meiotic chromosomes were observed in each presumed amphidiploid (method following Ebihara *et al.* 2005).
- 5) Plants with two or more different sterile genomic formulas, which differ only in their ge-

nomen dosage, are treated as a single hybrid taxon (so as to meet Art. H4.1, Appendix I, International Code of Botanical Nomenclature [Vienna Code] (McNeill *et al.* 2006) which states: When all the parent taxa can be postulated or are known, a nothotaxon is circumscribed so as to include all individuals (as far as they can be recognized) derived from the crossing of representatives of the stated parent taxa)—e.g. two different genomic formulas $\alpha\alpha\beta$ and $\alpha\beta\beta$ should be treated as a single hybrid taxon.

Scientific names related to Japanese plants

We examined the type specimens of the taxa belonging to the *Vandenboschia radicans* complex in Japan. Seven taxa were described from

Japan (*Trichomanes japonicum* Franch. & Sav. var. *japonicum*, *T. japonicum* var. *abbreviatum* H. Christ, *T. japonicum* var. *angustatum* H. Christ, *T. japonicum* var. *oshimense* H. Christ, *T. naseanum* H. Christ, *T. nipponicum* Nakai and *Vandenboschia subclathrata* K. Iwats.). Three taxa were described from Korea (*Trichomanes stenosiphon* H. Christ, *T. amabile* Nakai and *T. quelpaertense* Nakai). Three taxa were described from Taiwan (*Trichomanes kalamocarpum* Hayata, *T. somai* Nakai and *T. parvum* Copel.). *Trichomanes birmanicum* Bedd. was described from specimens collected in Myanmar, but Iwatsuki (1985) applied the name to Japanese plants.

Characters used in discriminant analysis

The following six characters were measured for each frond: 1) rachis length [RL]; 2) Stipe length [SL]; 3) Maximum lamina width [LW]; 4) Maximum width of stipe wing [WW]; 5) Diameter of rhizome [RD]; and 6) Number of lateral pairs of pinnae with branching veins [NP] (Fig. 1).

Three fertile leaves per collection were measured; the number of leaves measured was reduced accordingly for collections with less than three fertile leaves.

Discriminant analysis

Since it is unrealistic to determine the genome formula of old type specimens (ca. 80 to 130 years old) by DNA and ploidy analyses, the application of the names associated with the type specimens must be determined from their morphological features. Since most of the taxonomic characters, including shape of the sorus, are nearly uniform throughout the complex in Japan, discriminant analysis was performed using the following procedures.

- 1) The characters from the voucher specimens used in the study of Ebihara *et al.* (2005) and Ebihara *et al.* (2006b), plus 65 newly acquired samples (Appendix 1) were analyzed.
- 2) Computing discriminant coefficients: using the lda command of R 2.1.1.
- 3) Making a test data set: same characters as 1) were measured in the type specimens.

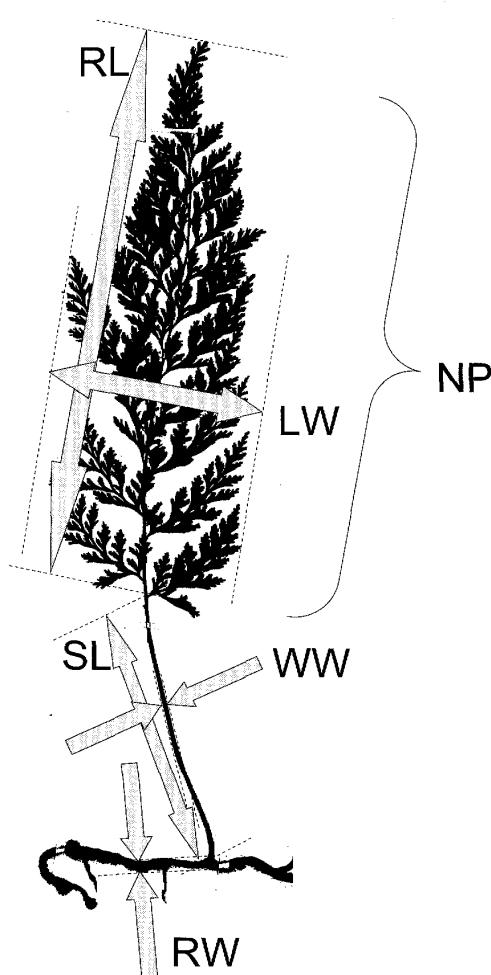


FIG. 1. Characters measured for discriminant analysis. RL: rachis length, SL: stipe length, LW: maximum laminar width, WW: maximum wing width of stipe, RD: diameter of rhizome and NP: number of pinna pairs.

- 4) Classification of test data: using the predict.lda command of R 2.1.1.
 5) Consideration of adequacy: If candidates were not narrowed down to one class, each upper candidate (posterior probability > 0.1) was considered about its adequacy by comparing locality and morphological features of the test sample (type specimen) to other specimens of each candidate class.

In general, hybrids exhibit characteristics intermediate between their parents, but those characteristics can vary between the two extremes (biased toward the mother or toward the father), which may distort the results. The final step of the procedure, therefore, took into account ambiguously classified samples.

We excluded genomic formulas with three or fewer training samples to avoid reducing the accuracy of discrimination; little effect on the analysis is assumed by excluding such minor taxa

from the classification because their small numbers reflect the extreme rarity of their populations.

Results and Discussion

Taxa redefined

Eight species and four hybrids are redefined following our policy for defining taxa (Fig. 2)—species AA (genomic formula: $\alpha\alpha/\alpha\alpha\alpha$); species A'A' ($\alpha\alpha$); species BB ($\beta\beta/\beta\beta\beta$); species CC ($\gamma\gamma/\gamma\gamma\gamma$); species AABB ($\alpha\alpha\beta\beta$); species AACC ($\alpha\alpha\gamma\gamma$); species BBCC ($\beta\beta\gamma\gamma$); species CCDD ($\gamma\gamma\delta\delta$); hybrid A*B ($\alpha\beta/\alpha\alpha\beta/\alpha\beta\beta$); hybrid A*C ($\alpha\alpha\gamma/\alpha\gamma\gamma$); hybrid B*C ($\beta\beta\gamma/\beta\gamma\gamma$) and hybrid ABC ($\alpha\beta\gamma/\alpha\alpha\beta\gamma/\alpha\beta\beta\gamma/\alpha\beta\gamma\gamma$).

Discriminant analysis

Measurements of morphological characters to use as a training data set were collected from 200

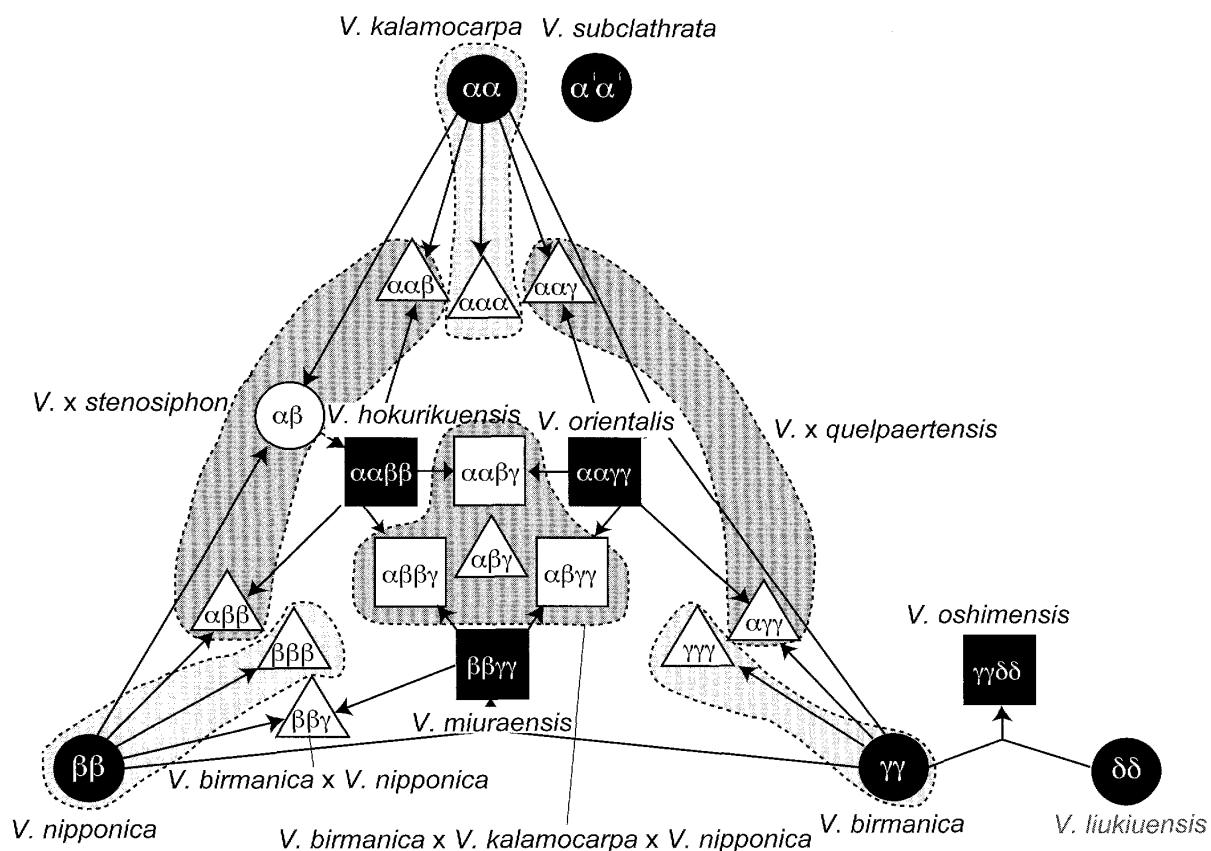


FIG. 2. A diagram of the presently recognized 12 taxa (8 species and 4 hybrids) of the *Vandenboschia radicans* complex with their reticulate evolution processes. *Vandenboschia liukiuensis* (Y. Yabe) Tagawa is usually not included in the complex. Shapes of the genomic formula symbols indicate ploidy levels. Circle: diploid, triangle: triploid, square: tetraploid. Colors of the symbols indicate presumable fertility. Black: fertile, white: sterile.

TABLE 1. Measurements of the training data. RL: rachis length, SL: stipe length, LW: maximum laminar width, WW: maximum wing width of stipe, RD: diameter of rhizome and NP: number of pinna pairs.

Taxon (class)	N	RL (mm)	SL (mm)	LW (mm)	WW (mm)	RD (mm)	NP
species AA	30	55.4 ± 20.6	28.4 ± 15.8	21.1 ± 6.6	1.1 ± 0.3	0.6 ± 0.2	9.2 ± 2.3
species A'A'	4	23.6 ± 9.3	7.5 ± 3.6	11.8 ± 3.0	0.8 ± 0.2	0.3 ± 0.0	5.3 ± 0.7
species BB	17	52.2 ± 14.0	20.7 ± 6.3	16.0 ± 4.4	0.7 ± 0.2	0.5 ± 0.1	11.5 ± 2.1
species CC	18	190.4 ± 40.0	77.0 ± 32.4	60.9 ± 12.3	2.2 ± 0.4	1.2 ± 0.2	18.3 ± 2.7
species AABB	12	55.5 ± 14.5	25.8 ± 9.4	21.6 ± 6.1	1.1 ± 0.2	0.6 ± 0.1	10.3 ± 1.4
species ACCC	17	120.3 ± 44.3	71.4 ± 28.5	44.0 ± 15.1	1.7 ± 0.4	1.0 ± 0.2	13.7 ± 2.6
hybrid A*B	83	61.7 ± 18.3	28.3 ± 13.4	21.4 ± 5.9	1.1 ± 0.3	0.7 ± 0.1	11.3 ± 1.9
hybrid A*C	19	129.0 ± 34.3	66.9 ± 26.2	40.8 ± 12.8	1.4 ± 0.3	0.9 ± 0.2	14.9 ± 1.9

samples (Table 1). Eight taxa (= classes) were used for the discrimination: species AA, species A'A', species BB, species CC, species AABB, species ACCC, hybrid A*B and hybrid A*C. The species CCDD was not included in this analysis because of its distinctive flared involucral lips, which allow easy taxon recognition). The remaining three taxa, species BBCC, hybrid B*C and hybrid ABC were also excluded from the analysis due to insufficient training data.

We performed linear discriminant analysis twice using a different data set each time. All six characters were included in the first analysis. The RD character, which is suggested to be the most effective coefficient, was excluded from the second analysis because the rhizome is lacking in the type specimen of *Trichomanes japonicum* var. *japonicum*. Results of the discriminant analyses are shown in Fig. 3 and Table 2. Measurements of the type specimens, and the predicted classification results are listed in Tables 3 and 4, respectively. For most of the type specimens, their first candidates are supported by a high posterior probability, indicating successful discrimination, while affiliations of the type specimens of *T. japonicum* var. *angustatum*, *T. nipponicum* and *T. kalamocarpum* are ambiguous since they have multiple candidates with low probabilities. We therefore deduced suitable classes for them by introducing other information. For *T. japonicum* var. *angustatum*, the flat (2-dimensional) fronds suggest that it is the same as hybrid A*B rather than species BB. The type specimen of *T. nip-*

ponicum was collected at Mt. Hakusan, Ishikawa Pref., in a mountainous area on the Sea of Japan side of Honshu, and within the distribution range of species BB. The type locality of *T. kalamocarpum* is Ali Shan in the central mountain range of Taiwan. Among its four candidate classes, the hybrid A*B was excluded because the β genome is unknown in Taiwan (Ebihara *et al.* 2005). Considering the fact that specimens of species AA collected at high elevations in Ilan Co., Taiwan bear a strong resemblance to the type specimen,

TABLE 2. Coefficients of discriminant axes (DA) of the training data. RL: rachis length, SL: stipe length, LW: maximum laminar width, WW: maximum wing width of stipe, RD: diameter of rhizome and NP: number of pinna pairs.

A: with all the six characters.

	DA1	DA2	DA3	DA4	DA5
RL	0.022	-0.026	0.056	0.027	0.036
SL	0.001	-0.006	-0.063	0.020	0.021
LW	0.014	0.001	-0.013	-0.004	-0.169
WW	1.457	-1.427	-0.202	-1.987	1.215
RD	2.157	1.125	-2.752	-1.920	1.056
NP	0.011	0.628	-0.165	-0.152	-0.148

B: without the rhizome character (RD).

	DA1	DA2	DA3	DA4	DA5
RL	0.025	0.020	0.053	0.042	0.032
SL	0.001	0.010	-0.069	0.003	0.026
LW	0.019	-0.002	-0.021	-0.016	-0.167
WW	1.723	1.321	-0.221	-2.487	1.581
NP	0.013	-0.621	-0.247	-0.278	-0.096

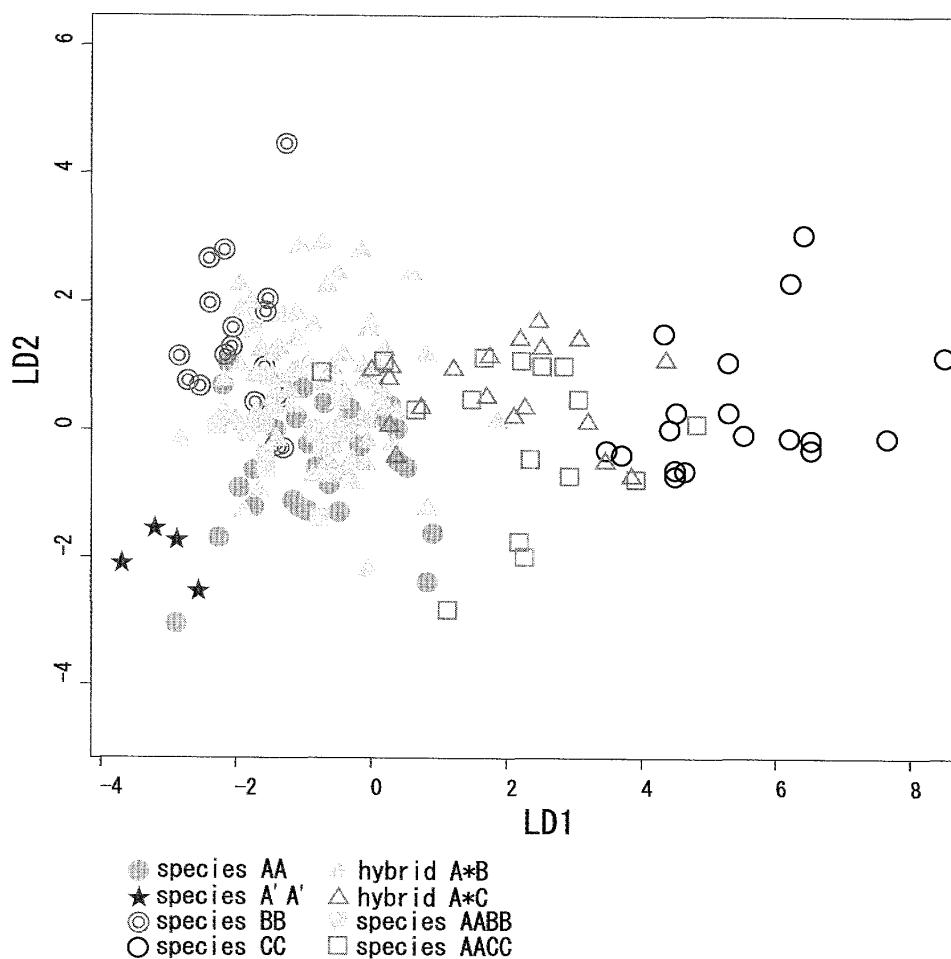


FIG. 3. A scatter diagram of the discriminated training samples with the linear discriminant 1 (X-axis) and the linear discriminant 2 (Y-axis). ●(orange): species AA, ★(purple): species A'A', ◎(blue): species BB, ○(red): species CC, ▲(green): hybrid A*B, △(orange): hybrid A*C, ■(green): species AABB and □(orange): species AACC.

TABLE 3. Measured values of type specimens for discriminant analysis. RL: rachis length, SL: stipe length, LW: maximum laminar width, WW: maximum wing width of stipe, RD: diameter of rhizome and NP: number of pinna pairs.

Taxon	Type specimen [Herbarium]	RL (mm)	SL (mm)	LW (mm)	WW (mm)	RD (mm)	NP
<i>T. japonicum</i> Franch. & Sav.	Savatier 1614bis [P]	84.7	60.1	40.0	1.85	NA	11.0
<i>T. japonicum</i> var. <i>abbreviatum</i>	Faurie 941 [P]	78.9	25.9	19.1	0.69	0.54	14.5
<i>T. japonicum</i> var. <i>angustatum</i>	Faurie 940 [P]	58.5	15.4	29.3	0.77	0.46	10.0
<i>T. naseanum</i>	Christ det. 1 [TI]	185.4	126.2	41.0	1.98	1.98	17.0
<i>T. nipponicum</i>	Yatabe & Matsumura s.n. [TI]	30.4	12.2	16.7	0.46	0.61	8.0
<i>V. subclathrata</i>	Koidzumi s.n. [KYO]	25.7	11.7	12.7	1.07	1.02	11.7
<i>T. stenosiphon</i>	Faurie 108 [KYO]	58.1	29.9	26.6	1.00	0.66	10.0
<i>T. amabile</i>	Taquet 5307 [TI]	60.8	27.4	18.2	0.91	0.91	11.0
<i>T. quelpaertense</i>	Nakai 1386 [TI]	199.7	120.9	33.5	1.64	0.94	17.0
<i>T. kalamocarpum</i>	Hayata & Sasaki s.n. [TI]	94.5	61.5	33.0	1.80	1.05	12.0
<i>T. somai</i>	Soma s.n. [TI]	174.0	36.0	42.0	1.20	1.80	13.0

TABLE 4. Results for predicting assignment of type specimens. Candidates are listed with their posterior probabilities.

Taxon (publ. year)		1st candidate	2nd candidate	3rd candidate	4th candidate	Final decision
<i>T. japonicum</i> (1879)	AACC	0.84				AACC
<i>T. japonicum</i> var. <i>abbreviatum</i> (1899)	BB	0.58	A*B	0.39		BB
<i>T. japonicum</i> var. <i>angustatum</i> (1899)	A*B	0.40	BB	0.23	AABB	0.19
<i>T. naseanum</i> (1905)	CC	0.86	AACC	0.14		CC
<i>T. stenosiphon</i> (1908)	A*B	0.60	AA	0.24	AABB	0.12
<i>T. amabile</i> (1914)	A*B	0.82				A*B
<i>T. quelpaertense</i> (1914)	A*C	0.91				A*C
<i>T. kalamocarpum</i> (1915)	A*B	0.29	AA	0.26	AACC	0.23
<i>T. somai</i> Nakai (1926)	CC	0.99				CC
<i>T. nipponicum</i> Nakai (1926)	A*B	0.39	BB	0.36	AA	0.14
<i>V. subclathrata</i> K. Iwats. (1958)	A'A'	0.77	AA	0.10	AABB	0.10
						A'A'

T. kalamocarpum probably belongs to the AA class. The type collection has little possibility of belonging to any of the rare taxa not included in the discriminant analysis according to our careful consideration of morphology and distribution. Consequently, the appropriate basionym for each taxon is as follows: species AA = *T. kalamocarpum*;

species A'A' = *V. subclathrata*; species BB = *T. nipponicum*; species CC = *T. birmanicum*; species AACC = *T. japonicum*; species CCDD = *T. japonicum* var. *oshimensis*; hybrid A*B = *T. stenosiphon* and hybrid A*C = *T. quelpaertense*. No names are available for species AABB, species BBCC, hybrid B*C and hybrid ABC.

Key to the species (excluding hybrids)

1. Lips of involucre distinctly dilated; fronds more than 25 cm long 8. *V. oshimensis* ($\gamma\gamma\delta\delta$)
1. Lips of involucre almost truncate; fronds less than 25 cm long
 2. Rhizome more than 0.8 mm in diameter
 3. Frond more or less 3-dimensional 7. *V. miuraensis* ($\beta\beta\gamma\gamma$)
 3. Frond completely flat
 4. Rhizome more than 1 mm in diameter 3. *V. birmanica* ($\gamma\gamma$, $\gamma\gamma\gamma$)
 4. Rhizome less than 1 mm in diameter 6. *V. orientalis* ($\alpha\gamma\gamma$)
 2. Rhizome less than 0.8 mm in diameter
 5. Lamina pale green; frond less than 5 cm long 4. *V. subclathrata* ($\alpha\alpha$)
 5. Lamina dark green; frond usually more than 5 cm long
 6. Segments definitely 3-dimensional 2. *V. nipponica* ($\beta\beta$, $\beta\beta\beta$)
 6. Lamina almost flat
 7. Lamina completely flat; plants often in evergreen forests on Pacific side of Japan
 - 1. *V. kalamocarpa* ($\alpha\alpha$, $\alpha\alpha\alpha$)
 7. Lamina more or less 3-dimensional; plants often in deciduous forests on Sea of Japan side or inland from Pacific side of Japan 5. *V. hokurikuensis* ($\alpha\alpha\beta\beta$)

Taxonomic treatment

*Diploid and autotriploid species***1. *Vandenboschia kalamocarpa* (Hayata) Ebihara, comb. nov.**

Basionym: *Trichomanes kalamocarpum* Hayata, Icon. Pl. Formosan. 5: 260, fig. 93 (1915). —Type. Taiwan, Ari-san, 1912, B. Hayata & S. Sasaki s.n. (holo- TI! [#00000611]; iso- TAIF!).

Trichomanes parvum Copel., Philipp. J. Sci. 51: 134, pl. 1, fig. 3 (1933). —*Vandenboschia parva* (Copel.) Copel., Philipp. J. Sci. 67: 53 (1938). —Type. Formosa [Taiwan], Tamsui Mountains, Sept. 4, 1881, W. Hancock 107 (holo- US!; fragment- U!).

Crepidomanes birmanicum sensu K. Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13: 530 (1985), p.p.

Japanese name. Haihoragoke.

Genomic formula. $\alpha\alpha$ and $\alpha\alpha\alpha$ (diploid and triploid).

Distribution. Japan: Pacific side of southern Honshu from Shizuoka Pref. to Shikoku, Kyushu, Yaku I., Okinawa I., Bonin Islands and Taiwan. The diploid occurs only in warm temperate regions along the Pacific coast (Mie, Wakayama, Osaka, Tokushima, Kochi prefectures and on Yaku Island).

Note. *Vandenboschia kalamocarpa*, formerly considered to be common in Japan, is in fact restricted to warm regions. Diploids are especially rare except on Yaku Island. Triploids, which are presumably sterile, tend to have slightly larger fronds than diploids, and show a wider distribution range than diploids. *Vandenboschia kalamocarpa* has also been found in Ilan and Taoyuan counties, northern Taiwan. The earliest name applicable to Japanese material with the genomic formulas $\alpha\alpha$ and $\alpha\alpha\alpha$ is *Trichomanes kalamocarpum*, described from Taiwan.

2. *Vandenboschia nipponica* (Nakai) Ebihara, comb. nov.

Basionym: *Trichomanes nipponicum* Nakai, Bot. Mag. (Tokyo) 40: 270 (1926). —*Vandenboschia radicans* (Sw.) Copel. var. *nipponica* (Nakai) H. Ito, J. Jap. Bot. 24: 127 (1949). —Type. Japan, prov. Kaga (Ishikawa Pref.), Mt. Hakusan, Aug. 6, 19??, R. Yatabe & J. Matsuura s.n. (holo- TI! [#00000235]).

Trichomanes japonicum Franch. & Sav. var. *abbreviatum*

H. Christ, Bull. Herb. Boissier 7: 817 (1899). —*Vandenboschia radicans* (Sw.) Copel. var. *abbreviata* (H. Christ) Kurata in Namegata & Kurata, Enum. Jap. Pterid. 260, 344 (1961). —*Lacosteopsis orientalis* (C. Chr.) Nakaike var. *abbreviata* (H. Christ) Nakaike, Enum. Pterid. Jap.: Filic. 24 (1975). —Type. Japan, Gwassan (Mt.Gassan, Yamagata Pref.), Sept. 28, 1898, U. Faurie 941 (holo- P!; iso- K!, KYO!).

Crepidomanes amabile sensu K. Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13: 531 (1985), p.p.

Japanese name. Hime-haihoragoke

Genomic formula. $\beta\beta$ and $\beta\beta\beta$ (diploid and triploid).

Distribution. Japan (endemic): Honshu (northern Tohoku district, the Sea of Japan side, Kanto (Chiba Pref., triploid) and inland Kyushu. Diploids are known only from Aomori, Akita, Yamagata, Niigata, Toyama and Oita prefectures.

Notes. *Vandenboschia nipponica* clearly shows the distribution of a Sea of Japan side element, but triploids are known from the Boso Peninsula, Chiba Pref., on the Pacific side. The most distinctive characteristic of this species is the 3-dimensionally arranged segments. Triploids, which are presumably sterile, often occur in the neighborhood of diploids.

3. *Vandenboschia birmanica* (Bedd.) Ching

Vandenboschia birmanica (Bedd.) Ching, Acta Phytotax. Sin. 8: 135 (1959). —*Trichomanes birmanicum* Bedd., Suppl. Ferns S. Ind. 3, t. 349 (1876). —*Crepidomanes birmanicum* (Bedd.) K. Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13: 530 (1985). —Type. Burma [Myanmar], Moulmain, Parish 181 (holo- K!).

Trichomanes naseanum H. Christ, Bull. Soc. Bot. France 52: Mém. I. 11 (1905). —*Vandenboschia radicans* (Sw.) Copel. var. *naseana* (H. Christ) H. Ito, J. Jap. Bot. 24: 124 (1949). —*Vandenboschia naseana* (H. Christ) Ching & Wang, Acta Phytotax. Sin. 8: 136 (1959). —*Trichomanes radicans* Sw. var. *naseanum* (H. Christ) Lellinger, Amer. Fern J. 58: 157 (1968). —*Lacosteopsis orientalis* (C. Chr.) Nakaike var. *naseana* (H. Christ) Nakaike Enum. Pterid. Jap.: Filic. 24 (1975). —*Crepidomanes radicans* var. *naseanum* (H. Christ) K. Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13: 530 (1985). —**Lectotype.** Japan, Kagoshima Pref., Amami-oshima, Naze, Dec. 4, 1900, Collector unknown, Christ determ. No. 1 (lecto- P, n.v.; isolecto- TI! [#00000194], **hic designatus**). Although two

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specimens, Mt. Omei, Continental China and Amami-oshima I., Japan, are cited in the original description, the latter should be chosen the lectotype, since the species' epithet is derived from Naze (Nase), a city of Amami-oshima. Although Iwatsuki (1985) cited only the specimen from Amami-oshima as the type, lectotype has not yet been designated.

Trichomanes somai Nakai, Bot. Mag. (Tokyo) 40: 267 (1926). —Type. Taiwan, Taipei Co., Rimmogan, May 7, 1916, T. Soma s.n. (holo- TI! [#00000197]).

Japanese name. O-haihoragoke.

Genomic formula. $\gamma\gamma$ and $\gamma\gamma\gamma$ (diploid and triploid).

Distribution. Japan: Honshu (Shizuoka and Wakayama pref., one locality known in each), Shikoku (Tokushima Pref., a single locality), southern Kyushu, Yaku I., Tokara Islands, Amami Islands, Okinawa I.; Taiwan; also on the Asian mainland (China to Nepal and India) and in Southeast Asia.

Notes. *Vandenboschia birmanica*, of tropical/subtropical Asia, is common from southern Kyushu southward in Japan, but rare in Honshu and Shikoku. The result of our discriminant analysis supports the validity of the thickness of the rhizome as a distinguishing character. *Vandenboschia birmanica* has the thickest rhizome of all the Japanese taxa of this complex. Ploidy analysis suggested the samples from Shizuoka and Tokushima have heavier genome sized than usual triploids of this species, thus they are possibly triploids.

Vandenboschia birmanica has sometimes been treated as a variety of the neotropical *V. radicans*, but they clearly differ in habit preference (epipetric in *V. birmanica* / hemi-epiphytic in *V. radicans*). Molecular evidence also supports the present treatment (Ebihara *et al.* 2005; unpublished data).

Iwatsuki (1985) applied the name *Trichomanes (Crepidomanes) birmanicum*, described from Myanmar, to medium sized Japanese plants corresponding to *Vandenboschia kalamocarpa* in our sense, but the Myanmar plants are probably smaller representatives of plants with the CC configuration. As a result, *V. birmanica*, which was formerly applied to species AA, is the correct name for species CC. Fraser-Jenkins (pers. comm.) has indicated that *Trichomanes striatum*

D. Don (Hamilton, 1825), described from Nepal, is an earlier name for *V. birmanica*. We prefer to use the name *V. birmanica* because the type material of *T. striatum* has not yet been found in any herbaria including BM, and also because it is difficult to judge from Don's description whether *T. striatum* is the same as *V. birmanica* or not.

4. *Vandenboschia subclathrata* K. Iwats.

Vandenboschia subclathrata K. Iwats., Acta Phytotax. Geobot. 17: 70 (1958). —*Trichomanes subclathratum* (K. Iwats.) C. V. Morton, Contr. U. S. Natl. Herb. 38: 182 (1968). —*Lacosteopsis subclathrata* (K. Iwats.) Nakaike, Enum. Pterid. Jap.: Filic. 25 (1975). —*Crepidomanes subclathratum* (K. Iwats.) K. Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13: 528 (1985). —Type. Japan, Okinawa Pref., I. Irumti [Iriomote I.], Jul. 1-20, 1923, G. Koidzumi s.n. (holo- KYO!; iso- US!).

Japanese name. Koke-haihoragoke.

Genomic formula. $\alpha\alpha$ (diploid).

Distribution. Japan (endemic): Iriomote Island.

Notes. This is the smallest species of this complex, and is locally abundant on Iriomote Island. Comparing the diploids of *Vandenboschia kalamocarpa*, this species is clearly distinguishable by the somewhat clathrate lamina and pale green fronds. Further study to determine their relationship is necessary.

Tetraploid (amphidiploid) species

5. *Vandenboschia hokurikuensis* Ebihara, sp. nov. (Fig. 4)

Species tetraploidea, hybridogena e *Vandenboschia kalamocarpa* et *V. nipponica*; differt a *V. kalamocarpa* stipitibus teretibus in parte inferiore; a *V. nipponica* frondibus latioribus et a *V. ×quelpaertensi* atque *V. ×stenosiphone* sporis normalibus.

Typus. Japan, Fukui Pref., Yoshida-gun, Eiheiji-cho, Komyoji, Y. Saito 040616-10 (TNS 779049).

Rhizomes long creeping, frequently branching, 0.4–0.7 mm in diameter, with dense blackish hairs, roots ca. 0.1 mm in diameter. Stipes (0.9–)2–4 cm long, upper portion winged, lower portion nearly terete, separate from adjacent stipes. Blade bipinnatifid, ovate to lanceolate, to 12 × 3.3 cm, apex acute to acuminate, glabrous, lateral pinnae

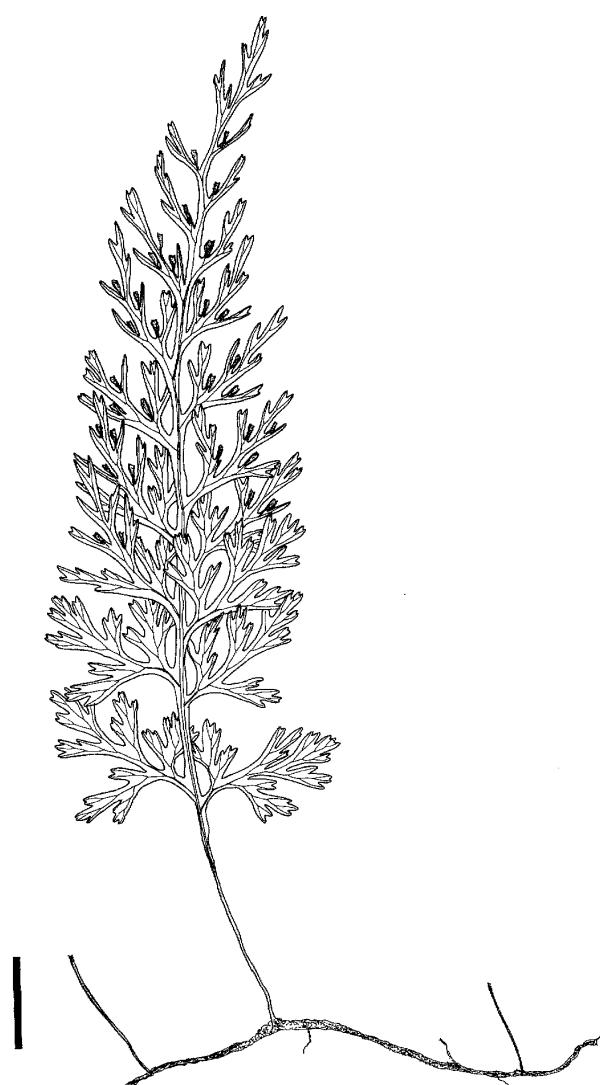


FIG. 4. *Vandenboschia hokurikuensis*, sp. nov. Y. Saito 040616-10 (holotype), scale = 1 cm, illustrated by A. Sasaki.

8–13 pairs, lower ones largest, to 2×1 cm, unequally deltoid to ovate. Sori tubular, $1\text{--}2 \times 0.5$ mm, involucres nearly truncate, receptacle long exserted on old fronds.

Japanese name. Hokuriku-haihoragoke.

Genomic formula. $\alpha\alpha\beta\beta$ (tetraploid).

Distribution. Japan (endemic), Honshu. Apparently common in the Hokuriku district.

Specimens examined. JAPAN. Saitama Pref.: Chichibu-gun, Ogano-machi, Han-nya, A. Ebihara 040404-01 (TNS). —Kanagawa Pref.: Yokosuka-shi, Taura-izu-mi-cho, T. Oka 50410-6 (TNS). —Niigata Pref.: Kamo-shi, Mt. Awagatake, A. Ebihara 000906-1 (TNS), Niitsu-shi, Shiratama-no-taki Fall, S. Ishizawa 040617-01 (TNS), Y. Tosaka 050402-01 (TNS); Kashiwazaki-shi, Oumigawa, S. Ishizawa 050429-01 (TNS). —Toyama Pref.: Nakaniikawa-gun, Kamiichi-machi, Ohiwa, M.



FIG. 5. $n = 72$ meiotic chromosomes of *V. hokurikuensis* (Y. Saito 040616-10, scale = 10 μm).

Ohta 040929-2 (TNS). —Fukui Pref.: Fukui-shi, Mt. Monju, K. Akai 040506-01, 040506-02 (TNS). —Shizuoka Pref.: Shimoda-shi, Shikine, S. Matsumoto 030412-2 (TNS). —Aichi Pref.: Nukata-gun, Nukata-cho, Natsuyama, A. Ebihara 031207-03 (TNS). —Mie Pref.: Iinan-gun, Iitaka-cho, Hachisu, K. Seto 61750 (TNS). —Nara Pref.: Yoshino-gun, Nishiyoshino-mura, Hikawase Riv., F. Kasetani 040110-01 (TNS), Tenri-shi, Takimoto-cho, F. Kasetani 040801-01 (TNS). —Kyoto Pref.: Kyoto-shi, Saigyo-ku, Izuriha-cho, F. Kasetani 040627-01 (TNS). —Hyogo Pref.: Hikami-gun, Aogaki-cho, Takitani, A. Ebihara 031014-01 (TNS). —Okayama Pref.: Katsuta-gun, Shoboku-cho, Okutsugawa Valley, K. Mizote 040626-01, 040918-02 (TNS). —Hiroshima Pref.: Hiba-gun, Takano-cho, Mt. Ohyorogi, N. Hamada 040500-01 (TNS). —Shimane Pref.: Nima-gun, Yunotsu-machi, Shimizudaishi, Y. Sugimura 030312-01 (TNS). —Yamaguchi Pref.: Yamaguchi-shi, Hosenji, A. Ebihara 040316-02 (TNS).

Notes. *Vandenboschia hokurikuensis* probably originated from hybridization between *V. kalamocarpa* and *V. nipponica*. It is extremely difficult to distinguish this species from the triploid hybrid *V. ×stenosiphon* by morphological characters alone, but *V. hokurikuensis* has regular spores and normal meiosis ($n = 72$) was observed in the

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type stock (Fig. 5). Besides, in most cases the pinnae tend to be less segmented than in *V. ×stenosiphon*, which gives the appearance of more loosely spaced lamina.

6. *Vandenboschia orientalis* (C. Chr.) Ching

Vandenboschia orientalis (C. Chr.) Ching, Fl. Reipubl. Popularis Sin. 2: 187 (1959). —*Trichomanes japonicum* Franch. & Sav., Enum. Pl. Jap. 2: 207, 618, (1879), non Thunb. in Murray, Syst. Veg., ed. 14: 941 (1784), nec Poir. in Lamarck, Encycl. 8: 79 (1808). —*Trichomanes orientale* C. Chr., Index Filic. 646 (1905). —*Vandenboschia radicans* (Sw.) Copel. var. *orientalis* (C. Chr.) H. Ito, J. Jap. Bot. 24: 125 (1949). —*Trichomanes radicans* Sw. var. *orientale* (C. Chr.) Lellinger, Amer. Fern J. 58: 157 (1968). —*Lacosteopsis orientalis* (C. Chr.) Nakaike, Enum. Pterid. Jap.: Filic. 23 (1975). —Type. Japan?, Savatier 1614bis (holo- P!). *Crepidomanes birmanicum* sensu K. Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13: 530 (1985), p.p.

Japanese name. Izu-haihoragoke.

Genomic formula. $a\sigma\gamma$ (tetraploid).

Distribution. Japan (endemic): Pacific coastal areas of Honshu (from Kanto region south), Shikoku and Kyushu, Sea of Japan side area of western Honshu (San-in district), Izu Islands, Bonin Islands, Yaku Island, and Tanegashima I., Tokara Islands, Amami Islands.

Notes. *Vandenboschia orientalis* originated from hybridization between *V. birmanica* and *V. kalamocarpa*. *Vandenboschia orientalis* is apparently intermediate between the parent species, but is often difficult to segregate from *V. ×quelpaertensis* only by morphology. One of the few distinguishing characters is the width of the rachis wings, which tend to be wider than in *V. ×quelpaertensis*. Both the normal spores and normal meiosis, with 72 bivalent chromosomes, (Mitui 1966) are the most reliable characters for recognizing *V. orientalis*. The type of *Trichomanes japonicum* Franch. & Sav. is an incomplete specimen consisting of only two fronds without a rhizome; its precise origin is unknown. Since the features of the fronds best match species AACC, *V. orientalis*, a substitute name for *T. japonicum* Franch. & Sav. is adopted for species AACC.

7. *Vandenboschia miuraensis* Ebihara, sp. nov. (Figs. 6, 7)

Species tetraploidea, hybridogena e *Vandenboschia bir-*

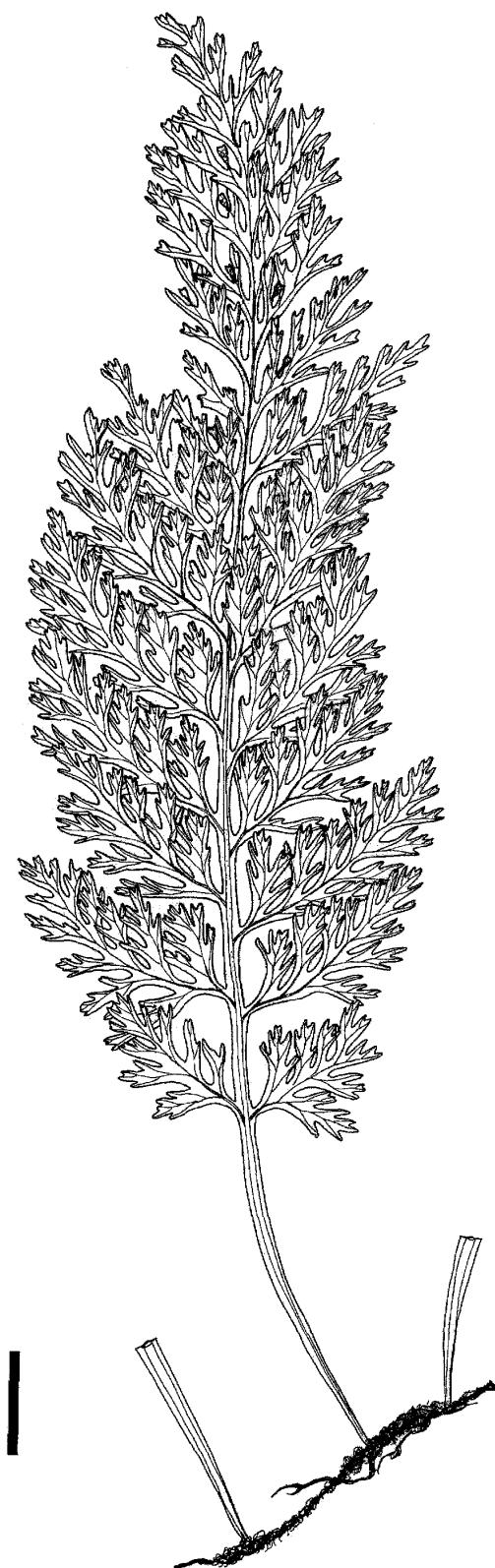


FIG. 6. *Vandenboschia miuraensis*, sp. nov. T. Oka 50410-1 (holotype), scale = 1 cm, illustrated by A. Sasaki.

manica et *V. nipponica*; differt a *V. birmanica* atque *V. orientali* segmentis tridimensionaliter dispositis, a *V. nipponica* frondibus majoribus et a *V. ×quelpaertensi* atque *V. ×stenosiphone* sporis normalibus.

Typus. Japan, Kanagawa Pref., Yokosuka-shi, Taura-izumi-cho, Apr. 10, 2005, T. Oka 50410-1 (TNS 777652).

Rhizomes long creeping, frequently branching, 0.8–1.0 mm in diameter, internodes 1–3 cm, densely covered with blackish hairs, roots ca. 0.2 mm in diameter. Stipes to 5 cm long, winged

throughout, upper portion ca. 1.8 mm wide, gradually reduced to base. Blade bipinnatifid, ovate to lanceolate, 15 × 4 cm, apex acute, glabrous, lateral pinnae ca. 15 pairs, those below middle largest, to 2.7 × 1.2 cm, unequally ovate. Sori tubular, 1–2 × 0.5 mm, lips of involucre slightly dilated, receptacle long exserted in old fronds.

Japanese name. Miura-haihoragoke.

Genomic formula. $\beta\beta\gamma\gamma$ (tetraploid).

Distribution. Japan (endemic): Honshu,



FIG. 7. *Vandenboschia miuranesis*. Photographed by A. Ebihara, at Taura-izumi-cho, Yokosuka-shi, Kanagawa Pref., the type locality.

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known only from the Miura Peninsula area, Kanagawa Pref.

Specimens examined. Kanagawa Pref.: Fujisawa-shi, Kawana, T. Oka 041103-01 (TNS), border of Fujisawa-shi and Kamakura-shi, Asahina, T. Oka 41211-1, 41211-2, 41211-3, 41211-6 (TNS).

Notes. *Vandenboschia miuraensis* is an amphidiploid species, probably originating from hybridization between *V. birmanica* and *V. nipponica*, an unusual combination of rarely geographically overlapping species. *Vandenboschia miuraensis* resembles *V. orientalis*, another tetraploid species, but has more or less 3-dimensional overlapping segments which reflect a characteristic of *V.*

nipponica. All collections other than the holotype are sterile juvenile plants.

8. *Vandenboschia oshimensis* (H. Christ) Ebihara, stat. nov. (Fig. 8)

Basionym: *Trichomanes japonicum* Franch. & Sav. var. *oshimense* H. Christ, Bull. Herb. Boissier 9: 1016 (1901). —Type. Japan, Amami-Oshima, Jul. 1900, U. Faurie 4635 (Holo- P?, n.v.; iso- KYO! [#00042390]).

Japanese name. Ryukyu-o-haihoragoke.

Genomic formula. $\gamma\gamma\delta\delta$ (tetraploid).

Distribution. Japan (endemic): Amami-Oshima I. (known only from the type) and Okinawa I.

Note. *Vandenboschia oshimensis* probably



FIG. 8. *Vandenboschia oshimensis* (T. Takara 040718-01, TNS). A. fronds; B. sori (scale = 1 mm).

originated from hybridization between *V. birmanica* and *V. liukiuensis* (Y. Yabe) Tagawa, although *V. liukiuensis* has been regarded as outside the *V. radicans* complex. Ebihara *et al.* (2005) discovered plants of hybrid origin between *V. liukiuensis* and *V. birmanica*. *Vandenboschia oshimensis* resembles *V. birmanica*, but is distinguishable by the larger frond, slightly flared mouth of the involucres, pale green fronds and rhizome sparsely covered with hairs. It is also distinguishable from *V. liukiuensis* by broader fronds (6–8 cm wide in *V. oshimensis* versus 2–3 cm wide in *V. liukiuensis*). Although the name *Trichomanes japonicum* var. *oshimense* has long been overlooked, morphological features of the type collection match the $\gamma\delta\delta$ tetraploids. No collections are known from Amami-Oshima Island other than Faurie's type collection.

Hybrids

The following taxa are presumed to be sterile hybrids that originated from crosses between sexually reproducing species in various combinations.

9. *Vandenboschia ×stenosiphon* (H. Christ) Copel.

Vandenboschia stenosiphon (H. Christ) Copel., Philipp. J. Sci. 67: 52 (1938), pro. sp. —*Trichomanes stenosiphon* H. Christ in H. Lév., Repert. Spec. Nov. Regni Veg. 5: 10 (1908). —Type. South Korea, Quelpaert [Cheju-do], Oct. 1908, U. Faurie 108 (holo- Pl; iso- KYO!).

Trichomanes japonicum Franch. & Sav. var. *angustatum* H. Christ, Bull. Herb. Boissier 7: 818 (1899), **syn. nov.** —*Vandenboschia radicans* (Sw.) Copel. var. *angustata* (H. Christ) K. Iwats. Acta Phytotax. Geobot. 17: 69 (1958). —*Lacosteopsis orientalis* (C. Chr.) Nakaike var. *angustata* (H. Christ) Nakaike, Enum. Pterid. Jap.: Filic. 24 (1975). —Type. Japan, Miyagi Pref., Matsushima, Aug. 15, 1898, U. Faurie 940 (holo- Pl; iso- KYO!, PE).

Trichomanes amabile Nakai, Bot. Mag. (Tokyo) 28: 65 (1914), **syn. nov.** —*Vandenboschia amabilis* (Nakai) K. Iwats., Acta Phytotax. Geobot. 17: 69 (1958). —*Crepidomanes amabile* (Nakai) K. Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13: 531 (1985). —Type. South Korea, Ins. Quelpaert [Cheju-do I.], Oct. 1911, T. Taquet 5307 (holo- TI! [#00000241]).

Crepidomanes amabile sensu K. Iwats., J. Fac. Sci. Univ.

Tokyo, Sect. 3, Bot. 13: 531 (1985), p.p.

Japanese name. Ko-haihoragoke.

Genomic formula. $\alpha\beta$, $\alpha\alpha\beta$ and $\alpha\beta\beta$ (diploid and triploid).

Distribution. Japan: Hokkaido, Honshu, Shikoku, Kyushu, Sado I., Oki I., Tsushima, and possibly Izu Islands and Yaku I.; South Korea.

Note. *Vandenboschia ×stenosiphon* contains the genomes of *V. kalamocarpa* and *V. nipponica*. This is the commonest among the taxa of this complex in Japan, and the size and shape of the frond are variable. The diploids, which are known only from a few localities in the Kanto district, have smaller fronds than the triploids

10. *Vandenboschia ×quelpaertensis* (Nakai) Ebihara, **comb. nov.**

Basionym: *Trichomanes quelpaertense* Nakai, Bot. Mag. (Tokyo) 28: 66 (1914). —Type. South Korea, Quelpaert [Cheju-do I.], T. Nakai 1386 (holo- TI! [#00042236]).

Crepidomanes birmanicum sensu K. Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13: 530 (1985), p.p.

Crepidomanes radicans var. *naseanum* sensu K. Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13: 530 (1985), p.p.

Japanese name. Seitaka-horagoke.

Genomic formula. $\alpha\alpha\gamma$ and $\alpha\gamma\gamma$ (triploid).

Distribution. Japan: Honshu (mostly on the Pacific side, from Kanto district west), Shikoku, Kyushu, Yaku I., Tanegashima, Amami-Oshima, Izu Islands, Bonin Islands., Okinawa I., Ishigaki I., Iriomote I. and Senkaku (Uotsuri) I.; South Korea (Cheju-do I.).

Note. *Vandenboschia ×quelpaertensis* contains the genomes of *V. birmanica* and *V. kalamocarpa*. The fronds are typically larger than in *V. ×stenosiphon*, and almost the same size as in *V. orientalis*. No specimen from South Korea other than the type collection have been examined.

11. *Vandenboschia birmanica* (Bedd.) Ching × *V. nipponica* (Nakai) Ebihara, **hybr. nov.**

Japanese name. Mitsuishi-haihoragoke.

Genomic formula. $\beta\beta\gamma/\beta\gamma\gamma$ (triploid).

Specimens examined. JAPAN. Chiba Pref.: Mt. Mitsushi, Kimitsu-shi, A. Ebihara 030225-01 (TNS). — Kanagawa Pref.: Asahina, Kanazawa-ku, Yokohama-shi, T. Oka 041106-01 (TNS).

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Distribution. Japan (endemic): Kanto district (Chiba and Kanagawa prefectures).

Note. A rare hybrid taxon known only from the Kanto district.

12. *Vandenboschia birmanica* (Bedd.) Ching × *V. kalamocarpa* (Hayata) Ebihara × *V. nipponica* (Nakai) Ebihara, hybr. nov.

Japanese name. Ai-haihoragoke.

Genomic formula. $\alpha\beta\gamma$ (triploid), $\alpha\alpha\beta\gamma$, $\alpha\beta\beta\gamma$, $\alpha\beta\gamma\gamma$ (tetraploid).

Distribution. Japan (endemic): Honshu (Chiba, Kanagawa, Shizuoka and Tottori prefectures) and Izu Islands (Aogashima I.).

Specimens examined. JAPAN. Chiba Pref.: Uchiura, Amatsukominato-machi, *A. Ebihara* 030225-03, (TNS, tetraploid). —Tokyo Pref.: Yasundo-go, Aogashima I., *T. Okamoto* s.n. (TNS, ploidy level unknown). —Kanagawa Pref.: Jinmuji, Zushi-shi, *A. Ebihara* 030725-03 (TNS, triploid). —Shizuoka Pref.: Rendaiji, Shimoda-shi, *M. Tanaka* 040403-02 (TNS, tetraploid). —Tottori Pref.: Imataki Fall, Yurihama-cho, *A. Ebihara* 041007-02 (TNS, tetraploid).

Note. This hybrid taxon comprises individuals with genomic formulas possessing three genomes (α , β and γ) probably produced by two hybridization events. The known distribution of the triploid is restricted to Kanagawa Pref. (Jinmuji), and the tetraploids are distributed on both the Pacific and Sea of Japan sides (Boso, Miura and Izu Peninsulas, Izu Islands and also in Tottori Pref.). The recognition of this hybrid, *Vandenboschia birmanica* × *V. kalamocarpa*, from its appearance is not an easy task, and tetraploids tend to occur in the neighborhood of the tetraploid parental species.

Conclusion

The *Vandenboschia radicans* complex in Japan was reorganized into 12 taxa (8 species and 4 hybrids) in accordance with genomic formula of

each. Discriminant analysis based on the morphological characteristics of the type specimens was used to determine the scientific name for each of the presently recognized taxa, except two for which no appropriate names exist. These taxa are therefore described as new species *V. hokuri-kuensis* and *V. miuraensis*.

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APPENDIX. Additional samples for collections of Ebihara *et al.* (2005) and Ebihara *et al.* (2006b). Sample data consist of sample code (in bold face), ploidy, genomic formula, voucher, and locality are provided for each sample. All the voucher specimens are deposited in TNS.

AK-5, 3x, $\alpha\beta\beta$, *Y. Horii* 041121-01, Akita Pref., Akita-shi, Nibetsu; **HG-6**, 3x, $\alpha\alpha\beta$, *K. Iwatsuki* 050700-01, Hyogo Pref., Yabu-shi, Ohya-cho, Mt. Hyonosen; **KC-7**, 3x, $\alpha\alpha\beta$, *S. Fujimoto* 041026-01, Kochi Pref., Motoyama-cho, Sogauchi; **KC-8**, 3x, $\alpha\alpha\gamma$, *K. Yamaoka* 041213-01, Kochi Pref., Aki-gun, Toyo-cho, Kawaguchi; **KG-12a**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050122-01, Kagoshima Pref., Amami-Oshima I., Naze-shi, Kinsakubaru; **KG-12b**, 4x, $\alpha^{**}\gamma$, *M. Takamiya* 050122-02, —; **KG-12c**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050122-03, —; **KG-12d**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050122-04, —; **KG-13a**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050122-05, Kagoshima Pref., Amami-Oshima I., Naze-shi, Chinaze River; **KG-13b**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050122-06, —; **KG-15a**, 4x, $\alpha^{**}\gamma$, *M. Takamiya* 050124-02, Kagoshima Pref., Amami-Oshima I., Sumiyo-son, Nishinakama, ; **KG-15c**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050124-01, —; **KG-15d**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050124-04, —; **KG-15e**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050124-06, —; **KG-16a**, 4x, $\alpha\alpha^*\gamma$, *M. Takamiya* 050124-08, Kagoshima Pref., Amami-Oshima I., Naze-shi, Asato; **KG-16b**, 4x, $\alpha\alpha^*\gamma$, *M. Takamiya* 050124-12, —; **KG-16c**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050124-07, —; **KG-16d**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050124-09, —; **KG-16e**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050124-10, —; **KG-16f**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050124-11, —; **KG-17a**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050122-07, Kagoshima Pref., Amami-Oshima I., Naze-shi, Koshuku River; **KG-17b**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050122-08, —; **KG-17c**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050122-09, —; **KG-17d**, 3x, $\gamma\gamma\gamma$,

M. Takamiya 050122-10, —; **KG-17e**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050122-11, —; **KG-18**, unknown, [γ/γ], *M. K. Kokubo* 041105006B, Kagoshima Pref., Amami-Oshima I., Sumiyo-son, Sumiyo; **NG-11**, 3x, $\beta\beta\beta$, *Y. Tosaka* 050129-01, Niigata Pref., Murakami-shi, Mt. Gagyu; **NR-14**, 3x, $\alpha^*\beta$, *K. Kawabata* 050700-01, Nara Pref., Yoshino-machi, Minami-narai; **OI-2a**, 3x, $\alpha^*\beta$, *M. Takamiya* 041124-01, Oita Pref., Amagase-machi, Jion-no-taki Fall; **OI-2b**, 4x, $\alpha^{**}\gamma$, *M. Takamiya* 041124-02, —; **OI-3a**, 2x, $\beta\beta$, *M. Takamiya* 041124-03, Oita Pref., Kusu-machi, Sozu, ; **OI-3b**, 2x, $\beta\beta$, *M. Takamiya* 041124-04, —; **OI-3c**, 3x, $\alpha^*\beta$, *M. Takamiya* 041124-05, **OI-3d**, 3x, $\alpha^*\beta$, *M. Takamiya* 041124-06, —; **OI-3e**, 3x, $\alpha^*\beta$, *M. Takamiya* 041124-07, —; **OK-10a**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050516-02, Okinawa Pref., Kunigami-son, Hentonai; **OK-10b**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050516-03, —; **OK-10c**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050516-04, —; **OK-11**, 3x, $\gamma\gamma\gamma$, *M. Takamiya* 050516-05, Okinawa Pref., Kunigami-son, Mt. Terukubi; **TS-7**, 3x, $\alpha\alpha\gamma$, *A. Narita* 1057, Tokushima Pref., Kainan-cho, Kuwabaradani; **TW-6**, unknown, [α], *S. Matsumoto* TW-702, Taiwan, Ilan Co.; **TW-7**, unknown, [α], *S. Matsumoto* TW-665, Taiwan, Ilan Co.; **WK-4**, 3x, $\alpha\alpha\alpha$, *K. Ueno* 050400-01, Wakayama Pref., Shirahama-cho, Gohji-dani; **WK-5**, 3x, $\alpha\alpha\gamma$, *K. Ueno* 050400-02, Wakayama Pref., Shirahama-cho, Ushiya-dani; **YM-1**, 2x, $\beta\beta$, *S. Takahashi* 050602-01, Yamagata Pref., Tsuruoka-shi, Tamugimata.